

LATE TERTIARY MUSTELIDAE (MAMMALIA, CARNIVORA) FROM
LANGEBAANWEG, SOUTH AFRICA

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(With 11 figures and 10 tables)

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ABSTRACT

The Mustelidae of the latest Miocene/early Pliocene Varswater Formation in 'E' Quarry, Langebaanweg, are described. They are identified as *Plesiogulo monspessulanus* Viret, 1939, which is the southernmost record of a wolverine, *Mellivora benfieldi* sp. nov., which is a likely ancestor of the living *M. capensis*, and *Enhydriodon africanus* Stromer, 1931, which is a structural and temporal intermediate between *E. lluecai* and *E. sivalensis*.

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INTRODUCTION

Since publication of an account of the Carnivora from the Varswater Formation in 'E' Quarry, Langebaanweg, Cape Province (Hendey 1974*b*), a great deal of additional material belonging to this order has been discovered (Hendey 1976*b*, 1977, 1978*c*). Although the original species list has not been substantially altered, the additional material does include specimens belonging to species not previously known from this locality and some which have led to revision of earlier identifications. Others have served simply to confirm original identifications.

Each of these situations applies in the case of the Mustelidae, a family which is comparatively poorly represented in the 'E' Quarry fauna, both in terms of numbers of species and numbers of specimens. Three species are recognized. The undescribed mustelid is the first African record of the extinct wolverine, *Plesiogulo* (Hendey 1976*b*: 239), the species previously incorrectly identified is a honey badger, *Mellivora* (Hendey 1974*b*: 68), while the species whose identity is confirmed is an otter, *Enhydriodon* (Hendey 1974*b*: 72).

The 'E' Quarry fauna, of which these three mustelids are a part, has generally been regarded as early Pliocene (4-5 Ma) in age. This dating is, however, insecure and present indications are that the outside age limits are 3.5 and 7 Ma, that is, the fauna dates from the very late Miocene and/or early Pliocene (Hendey 1978*c*).

The fossils dealt with in this report are from three distinct stratigraphic units in the Varswater Formation. They are, in descending order of age, the Quartzose Sand Member and beds 3aS and 3aN of the Pelletal Phosphorite Member (Hendey 1976*b*, 1978*a*). The durations of the intervals which elapsed between deposition of these units are not known, but they may have been appreciable. There is evidence, some of which will be presented below, that certain taxa show evolutionary advances over counterparts from lower units in the succession, although the differences are relatively slight and generally would not warrant taxonomic distinction at species level.

The material described is housed in the South African Museum, and catalogue numbers are prefixed SAM-PQ-, which identifies the institution and department concerned. This lettering is omitted from the text.

SYSTEMATIC DISCUSSION

Family **Mustelidae**

Subfamily Mellivorinae

Plesiogulo monspessulanus Viret, 1939

Material

L21570. Remains of an adult individual including: incomplete right mandible with P_3 to M_2 ; right I_1 and I^2 ; left I_1 and I^3 . Part of right pes including most tarsal bones, and metatarsals I to V lacking distal ends.

L40042. Remains of an adult male including: fragmented and incomplete skull and mandible with right P^1 to P^4 , right P_2 to P_4 , several worn incisors and fragments of other teeth. Elements of the vertebral column, limb girdles and all four limbs, most larger bones being incomplete.

L28394. Left mandible fragment with M_1 and M_2 .

Locality and horizon

Varswater Formation, 'E' Quarry, Langebaanweg. L21570 and L28394 are from the Quartzose Sand Member; L40042 is either from the Quartzose Sand Member or the lowermost level of bed 3aS of the Pelletal Phosphorite Member.

Age

Langebaanian (latest Miocene/early Pliocene), between 3,5 and 7 Ma.

Description

The most striking characteristic of this species is its large size. It was apparently only a little smaller than *Megalictis ferox* of the North American Miocene (Matthew 1907), which was the 'largest of all mustelids [reaching] the size of a black bear' (Kurtén 1971: 119). The Langebaanweg species is generally similar to the living wolverine, *Gulo gulo*, in terms of its dental and osteological characters.

The skull of L40042 was badly damaged by a mechanical excavator and useful observations can be made only on the upper and lower premolars, and

parts of the braincase, right maxilla and left mandible.

The maxillary fragment is comprised only of the bone immediately adjacent to the four premolars (Fig. 1). Parts of the alveoli of the \underline{C} and M^1 are preserved. The premolars are large and relatively broad compared with those of living



Fig. 1. Buccal and occlusal views of *Plesiogulo monspessulanus* maxilla (L40042) from Langebaanweg.

TABLE 1
Dimensions of the teeth of *Gulo gulo* and *Plesiogulo* species.

	P ¹		P ²		P ³
	<i>l</i>	<i>b</i>	<i>l</i>	<i>b</i>	<i>l</i>
<i>Gulo gulo</i> —Scandinavia (n = 11–15)*	4,0– 4,6	—	6,2– 7,2	—	9,6– 11,2
<i>Plesiogulo</i> 'major'—China†	—	—	—	—	—
<i>Plesiogulo monspessulanus</i> —Europe†	—	—	—	—	—
<i>Plesiogulo monspessulanus</i> —Langebaanweg L40042	c. 5,2	6,0	9,7	7,2	13,9
L21570	—	—	—	—	—
L28394	—	—	—	—	—
<i>Plesiogulo crassa</i> —China (means)†	—	—	8,2	5,9	11,0

* Data provided by E. Anderson (Denver, Colorado).

† Kurtén 1970.

Gulo gulo (Table 1). They are positioned as in the living species, except that P² and P³ overlap, which is unlike the fore-aft arrangement in the two available *G. gulo* comparative specimens and some illustrated examples (e.g. Anderson 1977, fig. 4; Novikov 1962, fig. 128; Kurtén & Rausch 1959, figs 3–4). Morphologically the teeth are similar to those of *G. gulo* in all observable respects. The infraorbital foramen of L40042 is more posteriorly situated than that of *G. gulo*. It opens above the apex of the P⁴ paracone, whereas in the living species the opening is above the anterior end of P⁴.

The features of the posterior parts of the skull of L40042 (Fig. 2) are essentially similar to their counterparts in *G. gulo*. The fossil skull is, however, very large (Table 2), with processes and crests greatly exaggerated. The sagittal crest is particularly prominent, being about 20 mm high along that part which is preserved. This crest terminates posteriorly above the level of the occipital condyles, whereas in *G. gulo* it usually, or always, projects further back. By contrast, the paroccipital process of the fossil projects further back than that of *G. gulo*.

The less posteriorly protruding sagittal crest is one manifestation of the relatively shorter braincase of the fossil. The distance between the external auditory meatus and most posterior part of the sagittal crest is about 30 mm in L40042, whereas in two *G. gulo* specimens it is 36 mm (SAM-ZM36095 ♂) and 40 mm (SAM-ZM38641 ♀). This difference is also indicated by the orientation of the nuchal crest in lateral view. In L40042 the lower part of this crest is at an angle of about 70° above the horizontal, whereas in the *G. gulo* comparative specimens the angle is about 50°.

In *G. gulo* the zygomatic process of the squamosal rises vertically above the level of the glenoid fossa so that the inferior margin of this process is elevated

P ¹	P ₂		P ₃		P ₄		M ₁		M ₂		
	<i>l</i>	<i>b</i>	<i>l</i>	<i>b</i>	<i>l</i>	<i>b</i>	<i>l</i>	<i>b</i>	<i>l</i>	<i>b</i>	
3-2	11,0-12,8	5,7-6,8	—	7,7-9,6	5,3-6,6	10,5-12,4	6,2-7,8	19,7-22,5	8,4-10,0	5,0-6,5	4,3-5,5
	—	8,9	—	12,5	—	14,3	—	30,5	11,3	—	—
	—	—	—	10,0	—	14,0	—	28,0	10,5	—	—
2	c. 15,6	9,1	6,7	12,6	8,1	16,0	9,5	—	—	—	—
	—	—	—	11,4	7,3	15,2	9,2	28,3	c11,0	11,4	c8,5
	—	—	—	—	—	—	—	c. 27,5	11,4	c. 7,5	c6,7
5	12,9	7,4	5,9	9,8	6,6	13,0	7,8	23,9	9,6	7,7	6,6

well above the glenoid fossa and external auditory meatus. In L40042 the process is much less elevated and its inferior margin is actually below the level of the auditory meatus.

Lower teeth of all three fossil individuals are preserved and the only elements not represented are I₂ to P₁. The lower teeth, like the uppers, are generally similar to their counterparts in *G. gulo*, although they are larger (Table 1, Fig. 3). The P₂ of L40042 differs from its counterpart in *G. gulo* in being single-rooted, a possibly significant character from a phylogenetic point of view and one which will be discussed later.

The M₁'s of both L21570 and L28394 are damaged and it cannot be established for certain whether or not a metaconid was present. Judging from the less damaged M₁ of L28394, this cusp was either very small or absent. The M₁ of the fossil does differ from that of *G. gulo* in having a relatively longer talonid.

The M₂'s of L21570 and L28394 are strikingly different in both size and morphology. The M₂ of the latter is slightly damaged, but it was evidently similar to that of *G. gulo* in proportions. By contrast, the M₂ of L21570 is anteroposteriorly elongated, with the trigonid and talonid distinguishable, although none of the individual cusps is prominently developed. The elongated M₂ of L21570 may be an individual peculiarity, rather than being typical of the Langebaanweg species. The M₁ : M₂ length ratio in L28394 (1 : 0,27) is comparable to the ratio in both living *G. gulo* (1 : 0,28 — n = 2) and the relatively primitive late Miocene *Plesiogulo crassa* (1 : 0,33—Kurtén 1970), whereas the ratio in L21570 is quite distinct from either (1 : 0,40).

The mandible of L21570 lacks much of the coronoid process and symphyseal region (Fig. 3). The latter region was affected by a pathological condition

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Dimensions of the teeth of *Gulo gulo* and *Plesiogulo* species.

	P ¹		P ²		P ³		P ⁴		P ₂		P ₃		P ₁		M ₁		M ₂	
	l	b	l	b	l	b	l	b	l	b	l	b	l	b	l	b	l	b
<i>Gulo gulo</i> —Scandinavia (n = 11–15)*	4,0– 4,6	—	6,2– 7,2	—	9,6– 11,2	5,7– 6,9	8,3– 9,2	11,0– 12,8	5,7– 6,8	—	7,7– 9,6	5,3– 6,6	10,5– 12,4	6,2– 7,8	19,7– 22,5	8,4– 10,0	5,0– 6,5	4,3– 5,5
<i>Plesiogulo</i> 'major'—China†	—	—	—	—	—	—	—	—	8,9	—	12,5	—	14,3	—	30,5	11,3	—	—
<i>Plesiogulo monspessulanus</i> —Europe†	—	—	—	—	—	—	—	—	—	—	10,0	—	14,0	—	28,0	10,5	—	—
<i>Plesiogulo monspessulanus</i> —Langebaanweg L40042	c. 5,2	6,0	9,7	7,2	13,9	9,0	c. 15,6	9,1	6,7	12,6	8,1	16,0	9,5	—	—	—	—	—
L21570	—	—	—	—	—	—	—	—	—	11,4	7,3	15,2	9,2	28,3	c11,0	11,4	c8,5	—
L28394	—	—	—	—	—	—	—	—	—	—	—	—	—	c. 27,5	11,4	c. 7,5	c6,7	—
<i>Plesiogulo crassa</i> —China (means)†	—	—	8,2	5,9	11,0	6,9	8,5	12,9	7,4	5,9	9,8	6,6	13,0	7,8	23,9	9,6	7,7	6,6

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The mandible of L21570 lacks much of the coronoid process and symphyseal region (Fig. 3). The latter region was affected by a pathological condition

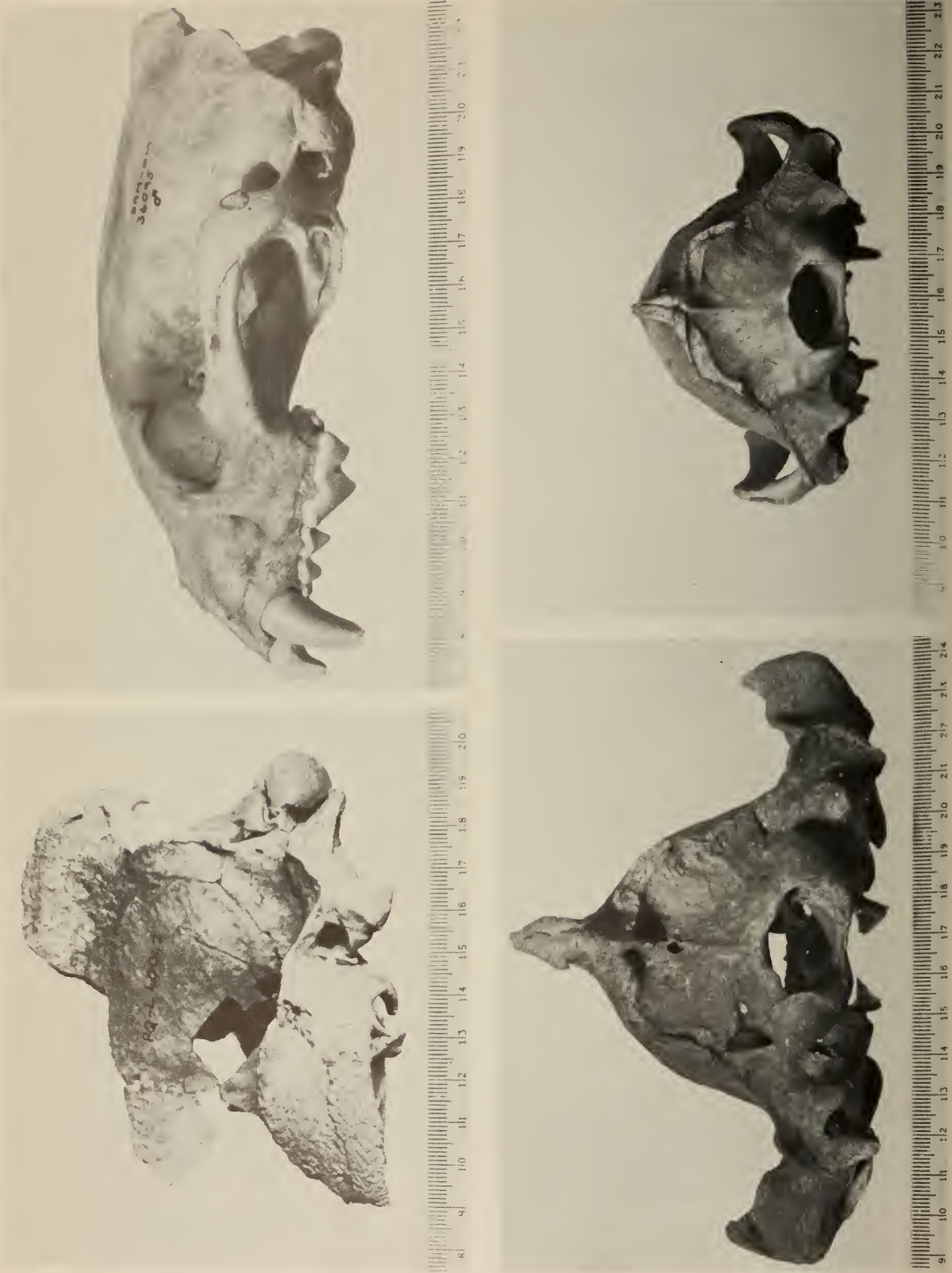


Fig. 2. Lateral and posterior views of *Plesiogula mouspessulanus* skull (L-40042) from Langebaanweg (left) and *Gutlo gutlo* skull (ZM36095) (right).

TABLE 2

Dimensions of the skull and mandible of the Langebaanweg *Plesiogulo monspessulanus* and living *Gulo gulo*.

	<i>Plesiogulo monspessulanus</i>			<i>Gulo gulo</i>	
	L40042	L21570	L28394	ZM36095	ZM38641
Braincase length (postorbital constriction to occipital condyles)	81,0	—	—	69,5	65,5
Width across occipital condyles	50,8	—	—	37,8	35,7
Mastoid width	108,2	—	—	88,8	81,4
Zygomatic width	158,5	—	—	103,7	95,0
Occiput height (occipital condyles to top of sagittal crest)	80,5	—	—	50,9	52,6
Depth of mandible below M_1	c. 39,0	39,0	37,5	23,3	22,3
Height of ascending ramus (angle to top of coronoid process)	68,7	—	—	50,9	47,1
Transverse diameter of condyle	44,1	41,4	—	25,7	24,7

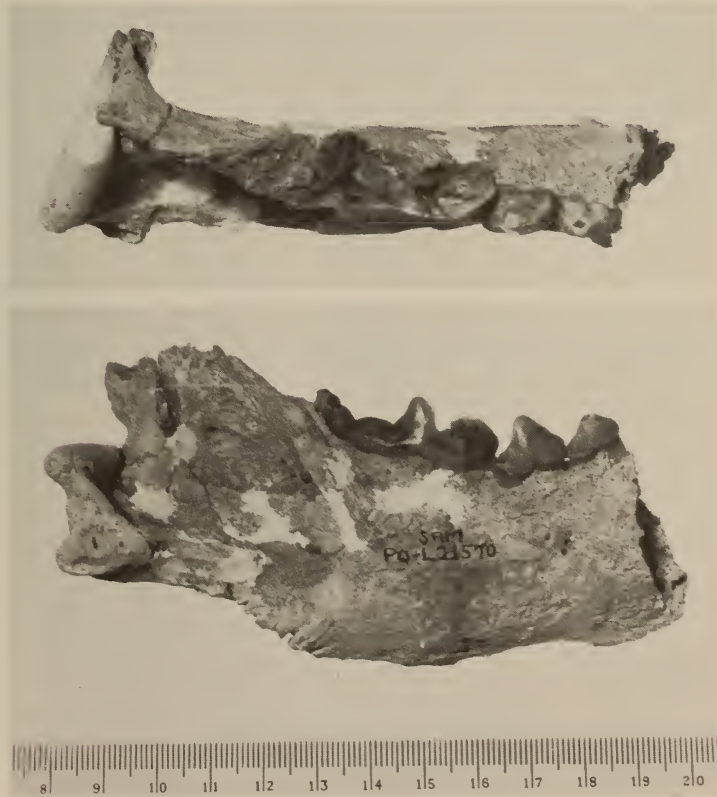


Fig. 3. Occlusal and buccal views of *Plesiogulo monspessulanus* mandible (L21570) from Langebaanweg.

which has left the remaining bone spongy in texture. The abnormality extends along the alveolar margins of the cheekteeth, becoming less pronounced posteriorly. The area of insertion of the occipito-mandibularis muscle in the subangular region is marked by V-shaped ridges of bone which diverge posteriorly, that on the buccal side being more prominent and irregular in outline. The counterparts of these ridges in L28394 and L40042 are only slightly developed, although the latter apparently belonged to a more aged individual, judging from wear on the cheekteeth. The ridges in L21570 may be a further manifestation of the mandibular pathology of the individual concerned.

The fossil mandibles are generally similar to corresponding parts of the mandibles of the *G. gulo* comparative specimens, except that the condyles are remarkably long and tubular in shape (Table 2, Fig. 4).

A feature of the dentition of L21570 which is evidently related to the pathological condition of the mandible is that, although the cheekteeth are only slightly worn, the preserved incisors are well worn. Similar pathology in one of the *G. gulo* comparative specimens (SAM-ZM38641) is accompanied by broken canines and heavily worn incisors. According to E. Granqvist of the Zoological Museum of the University, Helsinki (letter to R. Rau), damaged symphyseal teeth, and pathology of the adjacent parts of the jaws, are not uncommon in wolverines. Presumably this results from the aggressive behaviour and indis-



Fig. 4. Posterior view of *Plesiogulo monspessulanus* mandible (L40042) from Langebaanweg.

criminate feeding habits of the species. The condition of L21570 suggests that the late Tertiary wolverine from South Africa had habits similar to its living relative.

Ten of the vertebrae of L40042 are reasonably intact and all are distinguished from their modern counterparts only by their very much larger size. In general this also applies to other known postcranial bones of the fossil (Figs 5-6, Tables 3-6). The limb bones, and particularly the metapodials, are relatively less elongated, but much more stoutly proportioned than the corresponding bones in *G. gulo*. These differences, and possibly all others, are presumably due to the size difference between the species concerned. For example, the humerus of L40042 has a much deeper supratrochlea fossa and longer lateral condyloid crest, which reflect the stoutness and more heavily-muscled state of this bone. One of the differences for which no explanation can be offered is the marked curvature of the radius and ulna of L40042 (Fig. 6).

The relatively short and stout metapodials of the fossil go together with differences in proportions of certain carpal and tarsal bones. For example, the fossil calcanea and astragali are also relatively short and stout. Possibly the fossil species was more perfectly plantigrade than the living wolverine.

Postcranial bones of both L40042 and L21570 show signs of an arthritic condition, something which is not uncommon amongst the fossil carnivores from Langebaanweg (Hendey 1974b).

Fragments of the baculum of L40042 are preserved. They are similar in shape to corresponding parts of the baculum of *G. gulo*.

Discussion

The Mellivorinae are known from late Tertiary and Quaternary contexts through much of the Old World and North America. They are a heterogeneous group for which a subdivision into tribes has been suggested, and Webb (1969) visualized the subfamily as follows:

Mellivorini	Gulonini	Brachypsalini
<i>Aelurocyon</i> Peterson, 1906	<i>Ischyriactis</i> Helbing, 1930	<i>Paroligobunis</i> Peterson, 1906
<i>Megalictis</i> Matthew, 1907	<i>Hadriactis</i> Pia, 1939	<i>Brachypsalis</i> Cope, 1890
<i>Perunium</i> Orlov, 1947	<i>Plesiogulo</i> Zdansky, 1924	<i>Brachypsaloides</i> Webb, 1969
<i>Eomellivora</i> Zdansky, 1924	<i>Gulo</i> Frisch, 1775	
<i>Promellivora</i> Pilgrim, 1932		
<i>Mellivora</i> Storr, 1780		

At least one additional genus belonging to this subfamily (*Ferinestrix* Bjork, 1970) has since been described, while *Promellivora* has been regarded as a synonym of *Mellivora* (Hendey 1974b). The latter opinion may not have been warranted (see below).



Fig. 5. *Plesiogulo monspessulanus* from Langebaanweg and *Gulo gulo* (ZM38641).
 A. Humeri. B. Scapholunars. C. Pisiforms. D. Astragali. All specimens of *P. monspessulanus*
 belong to L40042, except the left astragalus which is of L21570.

TABLE 3
Dimensions of Langebaanweg *Plesiogulo monspessulatus* and living *Gulo gulo* long bones.

	HUMERUS		RADIUS		ULNA	
	<i>Gulo gulo</i> 6129*	<i>Plesiogulo</i> L40042	<i>Gulo gulo</i> 6129*	<i>Plesiogulo</i> L40042	<i>Gulo gulo</i> 6129*	<i>Plesiogulo</i> L40042
Max. length	—	—	—	—	145,0	186,0
Max. ant.-post. diameter, proximal end .	—	—	12,2	c15,5	—	—
Max. transverse diameter, proximal end .	—	—	17,5	c24,0	—	—
Max. ant.-post. diameter, distal end .	22,4	36,8	15,5	21,7	—	—
Max. transverse diameter, distal end .	39,8	54,5	23,2	34,1	14,4	c19,5

	FEMUR		TIBIA		FIBULA	
	<i>Gulo gulo</i> 6129*	<i>Plesiogulo</i> L40042	<i>Gulo gulo</i> 6129*	<i>Plesiogulo</i> L40042	<i>Gulo gulo</i> 6129*	<i>Plesiogulo</i> L40042
Max. length	14,9	c215,0	142,0	c185,0	129,0	162,0
Max. ant.-post. diameter, proximal end .	—	—	32,0	c50,0	—	—
Max. transverse diameter, proximal end .	40,0	59,0	—	—	—	—
Max. ant.-post. diameter, distal end .	—	—	17,5	26,4	14,0	19,6
Max. transverse diameter, distal end .	—	—	23,8	34,1	8,9	12,1

* U.S. Geological Survey, Menlo Park, Branch of Paleontology & Stratigraphy.

TABLE 4

Dimensions of Langebaanweg *Plesiogulo monspessulanus* and living *Gulo gulo* carpal and tarsal bones.

		<i>Gulo gulo</i>		<i>Plesiogulo monspessulanus</i>	
		6129*	ZM38641	L40042	L21570
SCAPIO- LUNAR	Max. transverse diameter	20,0	18,5	28,5	—
	Max. diameter proximal end to distal end	11,0	9,7	14,4	—
PISIFORM	Max. length	17,4	17,8	25,4	—
	Max. ant.-post. diameter, articular end	7,8	7,5	11,4	—
	Max. transverse diameter, articular end	11,9	10,5	18,5	—
CALCANEUM	Max. length	43,5	41,7	55,7	55,8
	Max. transverse diameter	22,0	22,0	33,1	33,2
	Max. dorsoventral diameter	22,4	21,0	31,7	—
ASTRA- GALUS	Max. length	27,0	26,8	36,1	36,4
	Max. transverse diameter, tibial facet	14,9	13,3	22,2	20,0
NAVICULAR	Max. length (dorsoventral diameter) .	15,8	—	23,3	22,3
	Max. transverse diameter	12,6	—	18,3	18,9

* U.S. Geological Survey, Menlo Park, Branch of Paleontology & Stratigraphy.



Fig. 6. Ulnae of *Plesiogulo monspessulanus* from Langebaanweg (L40042) and *Gulo gulo* (ZM38641).

TABLE 5
Dimensions of Langebaanweg *Plestiogulo monspessulanus* and living *Gulo gulo* metacarpals.

	METACARPAL I		METACARPAL II		METACARPAL IV	
	<i>Gulo gulo</i> 6129*	<i>Plestiogulo</i> L40042	<i>Gulo gulo</i> 6129*	<i>Plestiogulo</i> L40042	<i>Gulo gulo</i> 6129*	<i>Plestiogulo</i> L40042
Max. length	28,9	36,3	40,5	50,0	49,8	62,1
Max. ant.-post. diameter, proximal end .	6,8	7,0	8,7	14,4	10,2	15,0
Max. transverse diameter, proximal end .	8,8	8,0	7,4	11,1	7,4	12,0
Max. ant.-post. diameter, distal end .	6,4	6,2	7,9	12,2	8,6	12,2
Max. transverse diameter, distal end .	7,7	7,4	9,3	13,1	9,8	13,7

* U.S. Geological Survey, Menlo Park, Branch of Paleontology & Stratigraphy.

TABLE 6
Dimensions of Langebaanweg *Plestiogulo monspessulanus* and living *Gulo gulo* metatarsals.

	METATARSAL I				METATARSAL II			
	<i>Gulo gulo</i>		<i>Plestiogulo monspessulanus</i>		<i>Gulo gulo</i>		<i>Plestiogulo monspessulanus</i>	
	6129*	ZM38641	L40042	L21570	6129*	ZM38641	L40042	L21570
1. Max. length	—	—	—	—	49,9	50,4	56,2	—
2. Max. ant.-post. diameter, proximal end	9,5	8,3	—	10,2	9,2	9,0	13,8	14,6
3. Max. transverse diameter, proximal end	10,6	9,1	—	10,4	6,2	6,0	9,3	11,3
4. Max. ant.-post. diameter, distal end .	6,6	5,9	8,1	—	7,7	7,2	11,0	—
5. Max. transverse diameter, distal end .	7,8	7,3	9,7	—	9,4	8,9	12,6	—

	METATARSAL III			METATARSAL IV			METATARSAL V				
	<i>Gulo gulo</i>		<i>Plestiogulo monspessulanus</i>	<i>Gulo gulo</i>		<i>Plestiogulo monspessulanus</i>	<i>Gulo gulo</i>		<i>Plestiogulo monspessulanus</i>		
	6129*	ZM38641	L40042	L21570	6129*	ZM38641	L40042	L21570	6129*	ZM38641	L40042
1.	57,0	56,6	66,2	—	60,4	58,9	69,1	—	53,1	53,4	c59,0
2.	13,0	11,6	—	17,6	12,6	11,6	c17,0	17,8	—	—	—
3.	8,9	9,9	11,1	12,7	9,2	8,5	c12,0	12,5	—	—	—
4.	8,1	7,4	12,0	—	8,2	7,3	11,4	—	8,2	7,3	11,0
5.	10,0	9,4	13,2	—	10,1	9,3	12,9	—	10,0	9,0	11,9

* U.S. Geological Survey, Menlo Park, Branch of Paleontology & Stratigraphy.

With the exception of *Mellivora* and *Gulo*, all the recorded genera are late Tertiary in age and they are generally not well represented. As a result their inter-relationships are somewhat obscure. Webb (1969: 66) concluded that there was apparently 'an early Miocene radiation of mellivorine stock which gave rise to the *Aelurocyon*-*Megalictis* and *Paroligobunis*-*Brachypsalis*-*Brachypsaloides* lineages in North America and the *Ischyriictis*-*Hadriictis*-*Plesiogulo* lineage in Europe'. Later Mellivorini were confined to the Old World.

Plesiogulo, the genus with which the Langebaanweg wolverine is identified, was widespread in Eurasia during the late Miocene and Pliocene (Kurtén 1970), and was also present in North America (Kurtén 1970; Bjork 1970). Its presence at Langebaanweg near the southern tip of Africa means that it must have been distributed over much of this continent as well. Both Kurtén (1970) and Anderson (1977) regard *Plesiogulo* as the ancestor of *Gulo*.

Until recently large mellivorines were not known from Africa, but now, in addition to the Langebaanweg species, there is an as yet unidentified species recorded from the Omo Group deposits in Ethiopia (Howell & Petter 1976). The relationships between the Langebaanweg and Omo species have yet to be determined.

Of the described species of *Plesiogulo*, the one from Langebaanweg most closely resembles the broadly contemporaneous *P. monspessulanus* from Europe and *P. major* from China. These Pliocene species are the largest and most recent representatives of the genus. They are distinguished from one another only by the fact that *P. major* has an M_1 metaconid and Kurtén (1970: 12) concluded that they 'were obviously closely related'. They should, perhaps, be regarded as conspecific, with *P. monspessulanus* being the senior synonym. If this step is taken, then it becomes immaterial whether or not the Langebaanweg species had an M_1 metaconid, since there are no obvious grounds for separating it from its European and Chinese counterparts and all three may be identified with *P. monspessulanus*.

Geographical factors alone are sufficient to preclude the Langebaanweg *P. monspessulanus* from the role as direct ancestor of *Gulo*. In addition, it was noted above that the only preserved P_2 of this species is single-rooted and if this was characteristic of the Langebaanweg population, rather than just an individual anomaly, then it, too, indicates the lack of a direct phylogenetic connection with *Gulo*, in which P_2 is double-rooted. The P_2 of the Eurasian populations of *P. monspessulanus* has yet to be recorded.

Mellivora benfieldi sp. nov.

Holotype

L42838. Right mandible fragment with \bar{C} and P_2 to M_1 .

Referred material

L6385. Left mandible fragment with P_4 and M_1 (Hendey 1974b: 68-72, fig. 6).

L31273. Right mandible fragment with M_1 .

L50443. Right mandible fragment with P_4 and M_1 .

L50541. Right M^1 .

A left ulna (L40080) and right radius (L45384) are tentatively assigned to this species.

Other poorly preserved and/or fragmentary specimens were excluded from the present study.

Locality and horizon

Varswater Formation, 'E' Quarry, Langebaanweg. The holotype (L42838), L6385 and L40080 are from bed 3aS, and the remaining specimens are from bed 3aN, both units of the Pelletal Phosphorite Member.

Etymology

Named for Graham Benfield, formerly geologist and mine superintendent at the Chemfos Ltd mine at Langebaanweg, whose contributions to the Langebaanweg Research Project were of inestimable value.

Diagnosis

A species of *Mellivora* a little smaller than the extant *M. capensis*; P_1 and M_2 absent; P_2 to M_1 relatively narrow; principal cusps of P_2 to P_4 sharp-pointed, with sharp anterior and posterior keels; anterior and posterior accessory cusps of P_4 relatively small; M_1 talonid relatively short, narrow and sectorial; internal lobe of M^1 only slightly expanded, lacking prominent cingulum round the protocone; mandibular condyle not elevated above cheekteeth.

Age

Langebaanian (latest Miocene/early Pliocene), between 3,5 and 7 Ma.

Description

L6385 has already been described and discussed in detail (Hendey 1974b), and the paragraphs which follow summarize and supplement the earlier account of the Langebaanweg *Mellivora*.

The lower canine and cheekteeth of *Mellivora benfieldi* are superficially similar to those of the living honey badger, *M. capensis*. They differ in being smaller and narrower (Table 7), with cusps more sharp-pointed and keels more sharp-edged (Fig. 7). In these respects *M. benfieldi* is clearly the more primitive (less specialized) of the two species. They resemble one another in the number and arrangement of the teeth in the jaw and in the cusps on individual teeth. The P_4 accessory cusps are, however, smaller in *M. benfieldi*, while the M_1 talonid is smaller, narrower and without the basin-shaped depression situated lingually in *M. capensis*.

The internal (lingual) lobe of the isolated M^1 (L50541), like the M_1 talonid, is relatively small (Fig. 7). Its length (5,2 mm) is only slightly greater than that

of the buccal lobe (4,2 mm), whereas in *M. capensis* the corresponding figures are 8,3 and 4,4 mm (n = 8). The expansion of the internal lobe in the M¹ of *M. capensis* is due to the development of a prominent cingulum round the protocone, a feature which is lacking in L50541. The fossil tooth is also narrower



Fig. 7. A. Occlusal and buccal views of *Mellivora benfieldi* holotype (L42838). B. Occlusal view of M¹ (L50541). Both from Langebaanweg.

TABLE 7
Dimensions of mandibles and lower teeth of *Mellivora* species.

	\bar{C}		P ₂		P ₃		P ₄		P ₄ l : b		M ₁		M ₁ l : b		P ₂ -M ₁		Depth of corpus below M ₁		
	l	b	l	b	l	b	l	b	l	b	l	b	l	b	l	b	l	b	
<i>Mellivora capensis</i> (n = 8)	Mean	8,9	7,2	5,2	4,1	6,9	5,2	10,0	6,5	1:0,65	14,4	7,0	1:0,49	35,4	15,4				
	Range	7,6- 10,1	6,0- 8,4	4,5- 5,7	3,4- 4,7	6,3- 7,5	4,7- 5,6	9,5- 10,9	6,0- 7,6	1:0,60- 1:0,70	13,7- 16,3	6,4- 8,0	1:0,46- 1:0,51	33,7-38,0	13,7-17,8				
<i>Mellivora benfieldi</i>	L50443	—	—	—	—	—	—	8,4	5,2	1:0,62	12,6	6,0	1:0,48	—	cl4,5				
	L31273	—	—	—	—	—	—	—	—	—	13,5	6,1	1:0,45	—	14,6				
Bed 3as	L42838	6,5	4,6	4,6	3,4	6,2	4,4	8,4	4,8	1:0,57	11,5	5,3	1:0,46	30,2	13,4				
	L6385	—	—	—	—	—	—	9,4	5,3	1:0,55	14,1	6,0	1,043	—	15,8				
<i>Mellivora punjabiensis</i> *		11,6	8,5	5,3	—	6,1	4,2	8,4	6,2	1:0,74	—	6,0	—	—	18,3				

* Pilgrim 1932

than the M^1 of *M. capensis*, measuring 9,5 mm as against the mean of 10,9 mm in the comparative series.

The inferior margins of the fossil mandibles are slightly convex, whereas in the *M. capensis* comparative series they are straight or slightly concave. In both species the number and position of mental foramina are variable. In *M. benfieldi* there is only a slight elevation of the inferior margin towards the angle and the condyle is not raised above the level of the cheekteeth as in *M. capensis*. The larger of the fossil mandibles presumably belonged to males and are comparable in size to the smaller mandibles in the *M. capensis* comparative series, which belong to females.

The ulna, L40080 (Fig. 8), and radius, L45384, are the only postcranial bones in the Langebaanweg fossil assemblage which have so far been tentatively assigned to *Mellivora*. They are essentially similar to their counterparts in *M. capensis*, but are relatively short and stout (Table 8). Their size is in keeping with that of the lower jaws described above.

Discussion

It was earlier concluded that the 'E' Quarry *Mellivora* was closely related to, and possibly conspecific with, the Indian Mio/Pliocene *M. punjabiensis* (Hendey 1974b). It is now clear that the two species are not conspecific. *M. benfieldi* differs in having a smaller canine and shallower mandibular corpus, it lacks P_1 and has a narrower P_4 .

The loss of P_1 is an advanced character in mellivorines and in this respect at least, *M. benfieldi* is closer to *M. capensis*. Since the only known canine of *M. benfieldi* is probably that of a female (L42838), while the *M. punjabiensis* holotype could be a male, the canine size difference is not necessarily as great as would appear at first sight. Nevertheless, the difference is probably more than would be encountered in a single species. The large canine and relatively deep



Fig. 8. Ulnae of *Mellivora benfieldi* (L40080) from Langebaanweg and *M. capensis* (ZM36867).

TABLE 8
Dimensions of *Mellivora* species radii and ulnae.

	RADIUS		<i>Mellivora benfieldi</i> L45384	ULNA		
	<i>Mellivora capensis</i> ZM35574	<i>Mellivora capensis</i> ZM36867		<i>Mellivora capensis</i> ZM35574	<i>Mellivora capensis</i> ZM36867	
Max. length	106,8	101,4	80,4	139,0	130,5	<i>Mellivora benfieldi</i> L40080
Max. ant.-post. diameter, proximal end	12,1	11,7	9,4	—	—	—
Max. transverse diameter, proximal end	15,9	16,3	13,6	—	—	—
Max. ant.-post. diameter, distal end	13,9	14,2	13,4	13,5	14,8	13,3
Max. transverse diameter, distal end	24,0	22,7	17,8	8,5	8,6	9,0

mandibular corpus may also be primitive characters in *M. punjabiensis*, since they are features of *Eomellivora*, the genus from which *M. punjabiensis* may have been derived. The relatively short and broad P_4 of the latter is, however, more specialized than that of *M. benfieldi*.

To sum up, *M. punjabiensis* is an inappropriate structural ancestor for *M. benfieldi* and there was probably no direct phylogenetic connection between them. On the other hand, *M. benfieldi* is suitable in all observable respects to be ancestral to *M. capensis*. It follows that the suggestion, first made by Pilgrim (1932), that *M. punjabiensis* may have been an early ancestor of *M. capensis*, can now be dismissed. It also follows that the suggestion that the original separate generic status of '*M.* *punjabiensis*' was unwarranted (Hendey 1974b), is no longer acceptable. This species should once again be identified as *Promellivora punjabiensis*. The origins of *Mellivora* will be discussed again below.

The *M. benfieldi* sample is divisible into two units on stratigraphic grounds. The holotype (L42838) and L6385 are from bed 3aS of the Pelletal Phosphorite Member, while L31273 and L50443 are from the stratigraphically higher (and younger) bed 3aN. It was mentioned earlier that the interval between deposition of these beds may have been appreciable and that evidence exists of evolutionary changes in taxa common to both.

This applies in the case of *M. benfieldi*, since the P_4 's and M_1 's of the bed 3aN specimens are intermediate in breadth between those of the bed 3aS specimens and modern *M. capensis* (Table 7). In the case of M_1 's there are overlaps in the ranges of the three samples, but the mean figures show a breadth increase from the 3aS sample (1 : 0,45), through the 3aN sample (1 : 0,47), to *M. capensis* (1 : 0,49). The differences are thus in the expected order given the relative ages of the three samples. Although the mean values for both P_4 and M_1 are discrete, the differences are small and appreciable overlaps in ranges would be expected of larger samples.

It is worth noting here that the P_4 length : breadth ratio in *Promellivora punjabiensis* (1 : 0,74) sets this species apart from the *M. benfieldi*-*M. capensis* combination.

The new *Mellivora* specimens from 'E' Quarry confirm the earlier conclusion that the 'E' Quarry species is definitely not conspecific with the *Mellivora* from the nearby Beard's Quarry (Hendey 1974b, 1978a). The latter is clearly more advanced and closer to, if not conspecific with, *M. capensis*.

Subfamily Lutrinae

Enhydriodon africanus Stromer, 1931

Material

L9138. Right mandible fragment with part of P_4 (Hendey 1974b: 72-74, fig. 7).

L50000. Left mandible fragment with P_4 to M_2 and isolated left P^4 .

Various postcranial bones, including a femur (L41523), distal radii (L50001) and an astragalus (L50117), are tentatively assigned to this species.

Locality and horizon

Varswater Formation, 'E' Quarry, Langebaanweg. L9138 and L41523 are from bed 3aS, and the remaining specimens are from bed 3aN, both units of the Pelletal Phosphorite Member.

Age

Langebaanian (latest Miocene/early Pliocene), between 3,5 and 7 Ma.

Description

The mandible L9138 was described earlier and identified with *Enhyriodon africanus*, a species otherwise known only from Kleinzee, which is also on the west coast of the Cape Province, but about 400 km north of Langebaanweg (Hendey 1974b).

The new mandible, L50000, is a better specimen than L9138 and has served to confirm the identification with *E. africanus*, since it is very similar to the type specimen of this species. It lacks P₁, has a single-rooted P₂ and a double-rooted P₃. The P₄ has a principal cusp, a posterior accessory cusp and a prominent cingulum round its circumference. The P₄ of L9138 is higher crowned and has a more prominent posterior accessory cusp than those of L50000 (Fig. 9) and the *E. africanus* holotype. The significance of this difference will be discussed below.

The M₁ of L50000 is large, with the paraconid, protoconid and metaconid more or less equally developed (Table 9, Fig. 9). These cusps are low-crowned and bulbous. The talonid is large and basin-shaped, with the hypoconid covering about half its area. There is a prominent cingulum encircling the paraconid and extending posteriorly to the talonid on the buccal margin of the tooth. The M₂ is single-rooted and slightly elongated transversely, with little relief on the occlusal surface.

The isolated P⁴ (Table 9, Fig. 10), which evidently belongs to the same individual as the new mandible, is an important specimen since the P⁴ of *E. africanus* was not previously known. It has a small parastyle, the paracone is the most prominent cusp, the metastyle is very short, the protocone is large and nearly as prominent as the paracone and it is flanked posteriorly by a large, but low hypocone. There is a prominent cingulum encircling much of the tooth.

The various postcranial bones tentatively identified with *E. africanus* are similar to corresponding bones of the living clawless otter, *Aonyx capensis*. They are distinguished principally by their larger size. For example, the femur, L41523 (Fig. 11), has an overall length of 165 mm, compared with a mean length of 114 mm in a series of four *A. capensis* specimens.

Discussion

Repenning (1976) has dealt in detail with recorded representatives of *Enhyriodon* and concluded that there were two late Tertiary lineages of this genus. One led to *E. sivalensis* and 'can be characterized by the presence of a

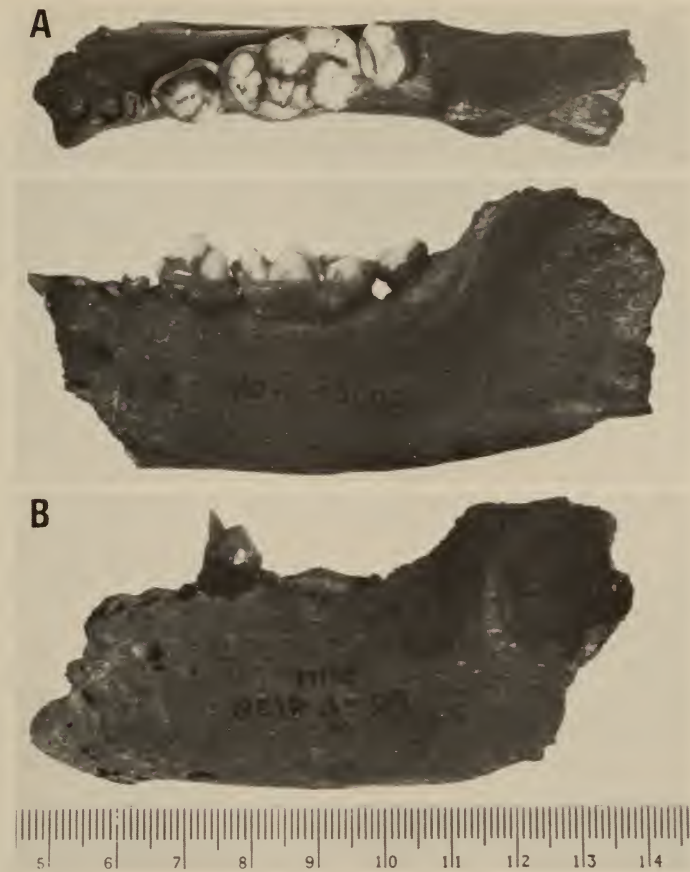


Fig. 9A. Occlusal and buccal views of *Enhydriodon africanus* mandible (L50000). B. Buccal view of *E. africanus* mandible (L9138) (reversed). Both from Langebaanweg.

parastyle on P^4 and by the location of the protocone of this tooth which is located as far lingually as the hypocone' (Repenning 1976: 305). The second lineage led to the living sea otter, *Enhydra lutris*.

On the basis of the P^4 characters, *E. africanus* evidently belongs with the group which includes *E. sivalensis*, a conclusion already reached by Repenning (1976) on other evidence. *E. sivalensis* is the more advanced of the two species, since it has a broader P^4 (Table 9), with a more quadrate outline due to a greater development of the hypocone. In addition, the cheekteeth of *E. africanus* apparently have more strongly developed cingula, which is a primitive condition in the *Enhydriodon/Enhydra* group.

E. africanus is here regarded as a structural and temporal intermediate

TABLE 9
Dimensions of the teeth and mandibles of *Enthyriodon* species.

	P ¹		P ¹ l : b		P ₄		M ₁		M ₂		P ₂ -M ₂ alveolar		Depth of corpus below M ₁		Breadth of corpus below M ₁	
	l	b			l	b	l	b	l	b	l					
<i>Enthyriodon sivalensis</i> * . . .	16,2	18,4	1 : 0,88		—	—	21,6	12,7	—	—	—		—		—	
<i>Enthyriodon africanus</i> † (Kleinsee)	—	—	—		11,9	8,6	22,0	+12,0	c9,5	—	57,0		27,0		14,8	
<i>E. africanus</i> (Langebaan- weg)	16,9	17,2	1 : 0,98		12,3	9,4	21,2	13,5	8,5	10,3	55,0		26,5		14,0	
bed 3aS L9138	—	—	—		c13,0	10,0	c22,0	c12,5	—	—	c55,0		30,1		17,7	
<i>Enthyriodon lluecai</i> * . . .	13,0	12,8	1 : 1,02		—	—	—	—	—	—	—		24,0		—	

* Reppenig (1976). M₁ is GS1 D161 — dimensions from Pilgrim (1932).

† Stromer (1931).



Fig. 10. Occlusal and buccal views of *Enhyriodon africanus* P₄ (L50000) from Langebaanweg.

between the late Miocene *E. lluecai* and the late Pliocene or early Pleistocene *E. sivalensis*.

A general trend in the evolution of *Enhyriodon* cheekteeth was towards inflation of the cusps and lowering of crown height, culminating in 'the low bulbous, or mastoid, tooth cusps', which are characteristic of *Enhydra* (Repenning 1976: 306). The fact that the P₄ of the bed 3aN L50000 has lower crowned and more bulbous cusps than the bed 3aS L9138 may therefore be interpreted as an indication that the former belongs to a more advanced form of *E. africanus*. This is further evidence which indicates that there was a lengthy



Fig. 11A. Femur of *Enhyriodon africanus* (L41523) from Langebaanweg. B. Femur of *Aonyx capensis* (ZM36254).

interval between deposition of beds 3aS and 3aN. The bed 3aN *E. africanus* is apparently morphologically closer to the Kleinzee representative of this species than is the one from bed 3aS.

GENERAL DISCUSSION

The Mustelidae comprise a relatively small element in the carnivore fauna of the Varswater Formation, being made up of only 3 of the approximately 29 recorded species (Table 10). In terms of the numbers of specimens known they form an almost insignificant part of the assemblage of carnivore material. Further collecting, and analysis of collected specimens, is unlikely to change this pattern of representation. Mustelids are a relatively uncommon element in the Pleistocene and Recent faunas of Africa as well.

The presence in the Langebaanweg fauna of an otter and a honey badger is not surprising, since both have counterparts in the modern fauna of the region, and Pleistocene representatives of these animals are also known (Hendey 1974b). The post-Pliocene species concerned are *Aonyx capensis* and *Mellivora capensis*, both of which were first recorded from the 'Cape of Good Hope' (Ellerman *et al.* 1953), the type specimens probably having come from the region in which Langebaanweg is located.

The only other mustelid, living or fossil, from this region is the musteline, *Ictonyx striatus*. It is still one of the more commonly occurring small carnivores in the vicinity of Langebaanweg. Small carnivores are well represented in the Varswater Formation fauna, but all are viverrids and the apparent absence of even one musteline is notable.

Wolverines are today known only from Arctic and sub-Arctic regions, so the presence of a fossil wolverine at Langebaanweg at about 33°S would seem at first sight to be extraordinary. It is, however, but one of several species in the Varswater Formation which have living counterparts on continents other than Africa. Other examples are a bear (Hendey 1972, 1977) and a peccary (Hendey 1976a). Such species belong to groups which had a much wider distribution in the Old and New Worlds during the late Tertiary than was the case subsequently. There was evidently appreciable faunal interchange between Africa and Eurasia at certain times during the late Tertiary. Greater climatic uniformity and differences in the pattern of zoogeographic barriers contributed to the existence of a more widespread and cosmopolitan fauna at that time.

The wolverines of that period were obviously not inhabitants of cold regions as they are today, and no satisfactory explanation can be offered for their failure to maintain their position other than in northern high latitudes. The living wolverine is a remarkably strong and resourceful animal, and one of the more extreme examples of an opportunistic feeder. It is difficult to conceive of its large late Tertiary forebears becoming extinct through unsuccessful competition with other carnivores or because of a decline and extinction of a preferred prey species. Similarly, since the wolverine today flourishes in the most rigorous of climates, the climatic deterioration late in the Tertiary, and

subsequently, is unlikely to have adversely affected its viability. The failure of the bear-like wolverine, and of true bears, to survive in Africa is one of the more curious aspects of the later history of mammals on this continent.

No such problems exist in the case of the honey badgers. *Mellivora capensis* is still found over much of Africa and parts of southern Asia (Dorst & Dandelot

TABLE 10
Carnivora of the Varswater Formation, Langebaanweg.

	Quartzose Sand Member	Pelletal Member bed 3aS	Phosphorite bed 3aN
Canidae			
<i>Vulpes</i> sp.		×	×
Ursidae			
<i>Agriotherium africanum</i>		×	×
Mustelidae			
<i>Plesiogulo monspessulanus</i>	×	?	
<i>Mellivora benfieldi</i>		×	×
<i>Enhydriodon africanus</i>		×	×
Phocidae			
<i>Prionodelphis capensis</i>	×	×	×
Viverridae			
<i>Viverra leakeyi</i>	×	×	×
<i>Genetta</i> sp.	×		
<i>Herpestes</i> sp. A	×	×	
<i>Herpestes</i> sp. B	×	×	
Herpestinae spp. C, D, E	×		
Herpestinae (not studied)		×	×
Hyaenidae			
<i>Acerocuta australis</i>	×	?	?
<i>Ictitherium preforfex</i>		×	×
<i>Hyaena abronia</i>	×	×	×
<i>Hyaenictitherium namaquense</i>	×		
<i>Euryboas</i> sp.	×	×	×
Hyaenidae sp. E		×	
Hyaenidae (not studied)		×	×
Felidae			
' <i>Machairodus</i> ' sp.	×		
<i>Homotherium</i> sp.	×	×	
<i>Felis</i> sp. (small)	×		
<i>Felis</i> aff. <i>issiodorensis</i>	×	×	
<i>Felis obscura</i>		×	
<i>Dinofelis</i> aff. <i>diastemata</i>	×	×	×
Felidae (not studied)		×	×
Unclassified Carnivora			
Gen. et sp. indet. (Canidae or Viverridae)	×		
Gen. et sp. indet. (?Procyonidae)	×		
Gen. et sp. indet. (?Lutrinae)	×		
Gen. et sp. indet. (?Otariidae)		×	